

# Description of a new genus with larviform females from Mauritius (Heteroptera, Enicocephalidae), with discussion of thoracic and abdominal morphology<sup>1</sup>

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**Abstract:** A new monotypic genus of Enicocephalomorpha (Enicocephalidae, Enicocephalinae), *Heissaptera janaki* nov.gen. et nov.sp., from Mauritius is established based on neotenously apterous females collected in litter of a mountain forest. The new genus belongs to a clade including genera with lateral Y-shaped and medial ⊥-shaped impressions (or their vestiges) on the midlobe of pronotum. Anatomy of exoskeleton of thorax is described in detail. Pterothoracic segments are fused in notal and sternal regions. The rudiments of larval forewing and hindwing pads are retained as small non-articulating lobes. Relationships of the new genus, occurrence of aptery in Enicocephalidae and neotenous aptery in the Heteroptera are summarized, and morphology of prothorax is discussed; the “proepimeral lobes” are identified as regions of notal rather than pleural origins. Metapostnotum and first abdominal mediotergite are modified as parts of a unique basiabdominal vibrational organ; presence of a vibrational basiabdominal system is synapomorphic for the Heteroptera.

**Key words:** Enicocephalidae, Enicocephalomorpha, *Heissaptera janaki*, Heteroptera, Mauritius, morphology, neotenous aptery, nov.gen. et nov.sp., taxonomy.

## Introduction

In this paper we describe a new genus and species of Enicocephalidae, Enicocephalinae, from Mauritius. The genus is represented by neotenously apterous females and fifth instar larvae of both sexes. Judging from the condition of wing pads in larvae, the unknown adult males are macropterous. Similar sexually dimorphic situation (and the apterous condition as such) was previously known in the Enicocephalinae only in the American genus *Hymenocoris* (WYGODZINSKY & SCHMIDT 1991). However, it is to be expected that flightless females will eventually be discovered in those subfamilies and genera of the Aenictopecheidae and Enicocephalidae which are based on males only and abound in Western Palearctic, Arabian peninsula and the Oriental region. All this, as well as relationship of the new

genus, is discussed within the context of the Enicocephalomorpha and/or Heteroptera.

The neotenous nature of the females of a new genus provided a great opportunity to study their external anatomy, which is, particularly in the thoracic region, admittedly modified by aptery but in other respects more plesiomorphic than that of macropterous forms owing to being closer to that of the larva. The major advantage of the apterous anatomy for study of the thorax is the retention of normal lateral and vertical position of pleural elements, while these are strongly diagonal, partly shifted dorsad and difficult to identify in macropterous enicocephalids (an analogy with dragonflies is not inappropriate). The opportunity has been fully utilized in the descriptive part of this paper, but is discussed in detail for the prothoracic notum and pleuron, and for wing rudiments only, while the other important

<sup>1</sup>Dedicated to Ernst Heiss, one of our best hemipterological friends, admired for accuracy of his work, broadness of his interests and charismatic personality.



**Figs 1-4:** *Heissaptera janaki* nov.sp., holotype, female. (1) Total view (total length 5.6 mm) (2) Head, lateral view (3) Pronotum and pterothorax, dorsal view (4) Pronotum and pterothorax, lateral view.

structural aspects with bearing on the morphology of Enicocephalomorpha and Heteroptera as a whole (such as pterothoracic fusions, position of scent gland openings and basiabdominal vibrational organ) are just mentioned and others (structure of abdomen and terminalia) omitted from the discussion entirely. There are several reasons for that. Some of the structures must be

studied on more extensive and disposable material, which we expect to receive, and some only in connection with the study of larvae, which we do not include in the present paper. We are not sure whether the two sympatric and syntopic females available are really conspecific and whether to ascribe the small but numerous differences (none affecting the gross morphology) between them to

intraspecific variation or to interspecific differences. For this reason we based the description, photographs and illustrations on the holotype only, and excluded the other material from the type series.

We were surprised not so much by the discovery of a new genus and species but rather by the number and importance of new structural information which could be extracted from a limited material.

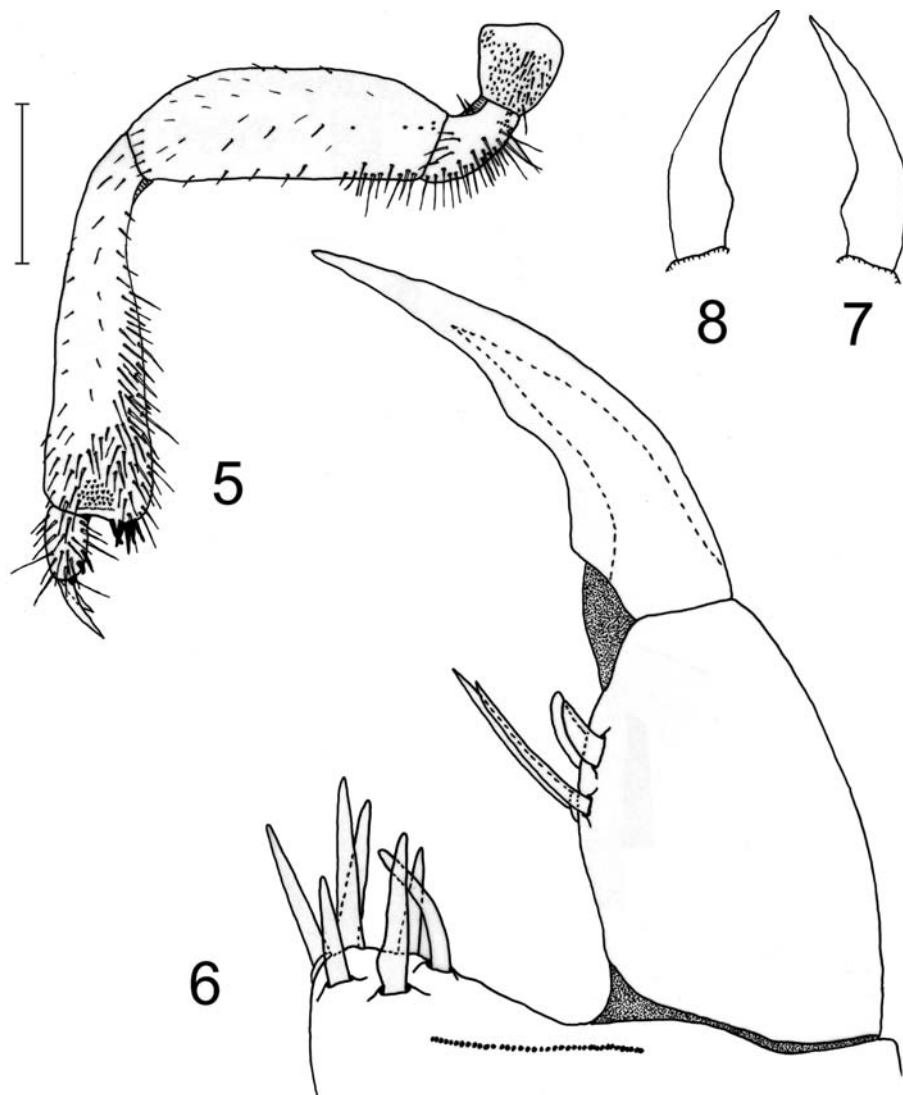
### Enicocephalidae: Enicocephalinae

#### *Heissaptera* nov.gen.

Type species. *Heissaptera janaki* nov.sp. by present designation.

**Etymology.** Named after Ernst Heiss, an eminent heteropterist, + apterous = wingless (from Gk. a = not + pteron = wing); gender feminine.

**Diagnosis.** Females neotenously apterous. Head strongly elongate, preocular part long, antennifers remote from eyes, the latter continuously faceted, postocular lobe delimited by a deep constriction, ocelli absent; dorsal surface of head nearly bare, ventral with long pilosity. Antennae thin, terete. Pronotum of three distinct lobes; the midlobe with sublateral Y-shaped impressions interrupting its hind margin, the mesal branch of Y terminating in a deep pit; hindlobe short, its posterior margin straight. Mesonotum and metanotum with short, projecting, non-articulating forewing and hindwing pads, respectively; mesonotum with a transverse, bulge shaped scutellum, metanotum with lateral spinous projections, mesopostnotum medially fused with metanotum. Mesosternum and metasternum broadly fused, the intersegmental sulcus lost. Metapostnotum, abdominal terga 1, 2 and ventrite 1 strongly modified owing to presumed presence of basiabdominal vibrational organ. Mediotergites 1 and 2 free. Abdomen with numerous setigerous tubercles, membranous, laterotergites delimited mainly by a system of sclerites. Tarsal formula 1-2-2. Fore coxae and trochanters without particulars, fore tibia once compressed, apicital armature of seven spiniform setae, the most dorsal one strongly curved, directed towards the cluster of straight ones; foretarsus with two, proximal, curved, spiniform setae and two distal platelets. Midtibia

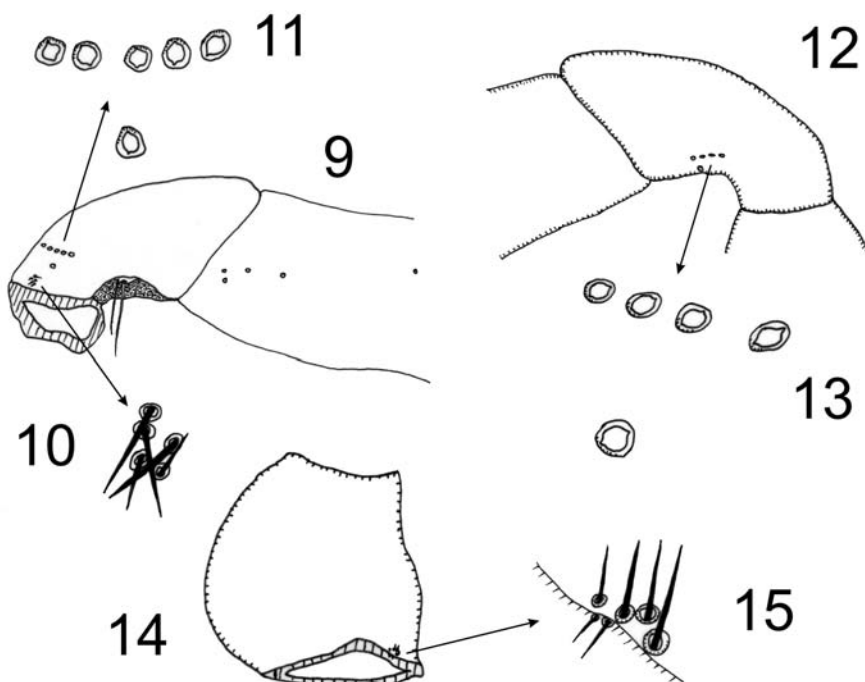


and hindtibia with two apical combs each. (Males winged as inferred from fifth larval instar, the latter with ocellar spots both in males and females.)

**Differential diagnosis.** There are only six genera of Enicocephalidae obligatorily apterous or with apterous females (all keyed by ŠTYS 2002b). *Heissaptera* differs from all of them by (1) wing rudiments developed as projecting lobes (rather than absent or represented by tubercles), (2) presence of medial ⊥-shaped and sublateral Y-shaped impressions on the midlobe of pronotum (absent in others), and (3) unique type of apicital armature of foretibia (as far as known). This is true also for females of an American genus *Hymenocoris* UHLER 1892, the only enicocephaline sharing with *Heissaptera* the sexually dimorphic female aptery; moreover, *Hymenocoris* females lack wing rudiments, their

**Figs 5-8:** *Heissaptera janaki* nov.sp., holotype, female, all anterior view. (5-7) Right foreleg (8) Left foreleg (5) Total view (bristle comb not illustrated); scale bar 0.5 mm (6) Apex of tibia and tarsus (7-8) Inner claw (6-8) hairs omitted.





**Figs 9-15:** *Heissaptera janaki* nov.sp., holotype, female, right foreleg (9) Trochanter and basis of femur (cleared, vestiture omitted except for coxal guard seta), anterior view (10) Condylar trochanteral organ, anterior view (11) Anterior trochanteral organ, anterior view (12) Trochanter, posterior view (13) Posterior trochanteral organ, posterior view (14) Coxa, anteromesal view (15) Coxal rim organ, anteromesal view (10-15) hairs omitted.

“proepimeral lobes”(= proepimera *partim* by WYGODZINSKY & SCHMIDT 1991) fuse mutually behind the forecoxae, and the forefemur is provided with a basidorsal process.

Only two specimens of *Oncylocotis* (*Vinsonicoris*) *mauriciensis* (VILLIERS 1969), both macropterous males, are known from Mauritius (VILLIERS 1969), and it is impossible to predict what the females of this species look like; however, the antennae of *O. (Vinsonicoris) mauriciensis* are strikingly thick, the body nearly unicolorous, light brown, and the head short and robust while in *Heissaptera janaki* nov.gen. et nov.sp. the antennae are unusually thin, the legs bicolorous, and the head long and slender. Moreover, no apterous *Oncylocotis* species is known, hence the identity of both taxa is improbable.

#### *Heissaptera janaki* nov.sp. (Figs 1-15)

**Material Examined.** Holotype ♀: [NW Mauritius, Le Pouce Mt., 16.-22.i.2006, 700-770 m, 20°11'48"S, 57°31'21"E, J. Janák lgt.], dry-mounted specimen, right foreleg in a vial associated with the specimen (to be placed in the collection of Department of Entomology, National Museum in Prague).

**Specimens excluded from the type series:** 1 ♀, same data, partly dissected; alcohol-preserved specimen: 2 ♂♂ larvae (fifth instar), 1 ♀ larva (fifth instar), same data; all in collection of P. Baňář (Praha). All specimens collected by sifting leaf litter.

**Etymology.** Named after Jiří Janák, Czech coleopterist, collector of the species.

**General facies** (Fig. 1) similar to Phthi-rocorinae, Monteithostolini. Elongate, robust, apterous, larviform; outlines of all supracoxalia visible in dorsal view. Head, thorax and extremities strongly, abdomen weakly, sclerotized.

**Measurements of the holotype** (in mm, L = length; W = width). Total L – 5.60; **head:** anterior lobe L – 0.80, posterior lobe L – 0.43, W – 0.51, distance eye-apex of antennifer – 0.44, diatone (max. W across eyes) – 0.48, min. interocular distance dorsal – 0.35, ventral – 0.35, eye L – 0.13; **labium:** total L – 0.82; **antenna:** segment 1 L – 0.28, segment 2 L – 0.70, segment 3 L – 0.67, segment 4 L – 0.64; **pronotum:** total L (max.) – 0.87, collum L (median) – 0.22, max. W – 0.64, midlobe L (median) – 0.51, max. W – 1.02, hindlobe L (median) – 0.14, max. W – 0.88; **foreleg:** forefemur L – 1.28, max. W – 1.28, foretibia L – 1.13, max. W – 0.37; **midleg:** midfemur L – 0.95, max. W – 0.20, midtibia L – 1.04, max. W – 0.12, midtarsus L (without claw) – 0.35, max. W – 0.07; **hindleg:** hindfemur L – 1.33, max. W – 0.33, hindtibia L – 1.47, max. W – 0.12, hindtarsus L (without claw) – 0.48, max. W – 0.08.

**Coloration** variegated, ranging from straw colored through various hues of brown to black, not forming distinct patterns. Head brown, lateral and ventral parts dark-brown. Collum dark-brown, midlobe of pronotum yellowish (contrasting), the rest of prothorax brown, lateral parts of collum and supracoxal lobes blackish (contrasting), metepimeron yellowish. Pteronotum dull, forewings, pleura and supracoxal lobes blackish to black. Antennal segment 1 dull straw colored, 2, 3 and proximal half of 4 as well as labium brown, distal part of antennal segment 4 non-contrastingly yellow-brown. Legs bicolorous, trochanters and knees pale. Forelegs brownish, long knees straw coloured, apical third of foretibia dark-brown. Mid- and hindlegs dull-brownish, coxae and trochanters straw colored, knees much paler. Abdomen dark-brown to blackish (small isolated sclerites, terminalia).

**Cuticle.** (Nearly transparent except for melanic parts, hence color patterns some-

times difficult to assess.) Head, collum, mid-lobe of pronotum, propleuron and all the supracoxal lobes, as well as legs, smooth, strongly lustrous; hindlobe of pronotum, pteronotum and pteropleura (excl. supra-coxalia) moderately lustrous, mostly with shallow and irregular puncturation, some areas with transverse wrinkles (hindlobe of pronotum). Abdomen matt, with shallow, dense and irregular puncturation and minute setigerous tubercles all over. **Special features:** (1) All the mesal surface of fore-coxa matt, finely shagreened. (2) Anterior mesosupracoxale with deep, longitudinal wrinkles.

**Vestiture** whitish to golden; no primary chaetotaxy except on legs. **Dorsum** of head and thorax nearly bare, with extremely short vestiture, contrasting with densely pilose lateral and ventral sides. Head and pronotum with a few appressed, usually curved to scale-like, extremely short hairs, but with a dense, almost tomentose, short pilosity in all transverse depressions (the very short hairs might be microtrichia – no alveoli observed). Only the anteriormost part of head (in front of antennifers) modally covered with dense, long, curved hairs. Pterothorax with moderately dense, very short, erect bristly hairs, most distinct and densest on mesopostnotum. **Lateral sides and venter.** Lateroventral and ventral sides of head densely covered with short, straight and appressed hairs, extremely abundant and long in postocular constriction, tending to become erect at the postocular lobe. In addition, the ventral surface with many long, soft, straight to moderately curved, erect hairs of varying length; the longest hair in the middle of postocular lobe slightly longer than the height of head. Anterior and posterior sectors of the lateroventral face of collum densely covered with short hairs directed cephalad and caudad, respectively. These collar hairs forming a nearly tomentose cover on ventral face beneath the collar tubercles, being accompanied by straight or curved hairs of a variable direction. All pleural sclerites (including all supra-coxalia) nearly bare, with few minute appressed hairs, only the anterior surface of anterior prosupracoxale with a long and dense cover of anteriorly directed hairs (merging with those of the collum) and the posteriormost surface of posterior prosupracoxale with

scattered, short but outstanding curved hairs. Ventral part of collum and anterior part of prosternum with dense, curved hairs, posterior part of the latter nearly bare. Ventral part of mesoprecoxale densely pilose, while the mesosternum nearly bare, with a few scattered short hairs. Metasternum bare. **Abdomen.** Dorsum uniformly covered with dense, short, blackish, mostly straight, very short, usually appressed hairs, mostly arising from minute setigerous tubercles. These hairs become very long on terminalia and venter, being still appressed or strongly diagonally outstanding. **Antennae.** Segments 1-4 with short (always shorter than segment diameter), straight or rarely curved, appressed to diagonal hairs; on each segment, these hairs becoming denser, more regular and less appressed in proximo-distal direction. Segment 2 with one long, subterminal, ventral, thin and erect trichobothrium-like hair, its dorsal apex with a group of 6-7 more diagonal and thicker long hairs; 3 with about 11-14 long, erect, thin but stiff hairs distributed rather regularly along the segment, pointing in all directions (like in most Dipsocoromorpha); 4 with about 20 such hairs. All the **labium** densely covered with long, diagonal, straight hairs, interspersed with more erect, longer and thinner trichobothrium-like macrotrichia. **Forelegs.** Pilosity longer and denser than on mid- and hindlegs; dense and long pilosity of trochanters, contrasting with that on the other segments, particularly striking. Coxa with two ventral, thin, long and erect trichobothrium-like setae (tr-setae further on). Dorsal face of trochanter nearly bare, except for two curved basal setae; anterior, posterior and ventral faces with extremely dense and long, curved hairs including also over 10 tr-setae. Femur: anterior and dorsal faces nearly bare, the latter with a few very short erect setae; proximal parts of posterior and ventral faces with long diagonal pilosity (continuation of that on the trochanter) with about five ventral and two isolated posterior tr-setae. Tibia: dorsal face with some short erect hairs and interspersed several tr-setae (the apical one very long and conspicuous), the ventral face and distiventral and apical parts of lateral faces with abundant dense and long pubescence intermixed with many erect tr-setae directed anterad, posterad and ventrad. Anterior face with an apical tri-

angle (Fig. 5) of minute, scale-like setae. Tarsus with long, suberect pilosity formed mainly by tr-setae. **Midlegs:** Pubescence short and scarce, appressed to diagonal, straight to curved, with a few admixed tr-setae (coxa – one distiventral, trochanter – one medioventral and one anteroproximal, femur – 1+1 subproximal). Tibia with a short diagonal pubescence, particularly dense on ventral surface; tr-setae: one basidorsal, one apicidorsal, one ventral medial (diagonal) and one ventral subapical. Distal segment of tarsus with dense and long, diagonal ventral and distidorsal macrotrichia. **Hindlegs:** pubescence similar to that of midlegs, but tr-setae scarcer (rubbed off?; coxa – one posteroventral, trochanter – one conspicuous basiventral, tibia – two posterior, subapical).

**Head** (Fig. 2). Anterior lobe strikingly long, cylindrical, preocular lateral margins subparallel, antennifers much distant from eyes, prominent. Eyes small, subhemispherical, of about 25 facets, the anterior facets closely packed and separately convex, the posterior ones distant, flat and difficult to recognize; eyes in lateral view more distant from dorsal than ventral margin of head; 2-3 short, curved interommatidial setae present. Dorsal and ventral ocular indices identical: 7.4. Postocular constriction deep. Postocular lobe subglobular, slightly transverse (1.2 times as wide as long), widest in the middle, with a linear, impressed midline (visible under strongly diagonal illumination only). Ocelli absent.

**Antennae** (Fig. 1). Long and thin, antennal formula (longest segment first) 2-3-4-1 (length differences 2, 3, 4 small). Segment 1 rather thick, cylindrical, strongly surpassing apex of head; 2 terete, slightly thickened distad; 3 slightly narrower than 2, uniformly terete; 4 narrowly fusiform. **Labium** (Fig. 2). Relatively thin, directed caudad, diagonal, reaching postocular constriction. Labial formula 3-4-2-1. Lateral view: segment 1 thick, with all the ventral surface telescoped within head capsule (or absent?); 2 medially slightly constricted, strongly widening distad; 3 thin, topographically ventral outline straight, the dorsal one basally deeply concave (constricted), then moderately convex throughout; 4 conical, sharply tapering.

## Thorax (Figs 3-4).

**Pronotum and propleuron** with sharply delimited components. **Collum** ring-shaped, its dorsal face subdivided by a percurrent, linear, impressed median; a short anterior part (= **precollum** *sensu* ŠTYS & BAŇAŘ 2006) depressed, posterior part bulging; lateral face produced gradually in a pair of prominent tubercles, these sharply demarcated from the ventral side at the level of pleural elements of the mid-lobe. **Midlobe, dorsum.** Surface convex, inflated, very broad (much wider than collum and the posterior lobe), laterally rounded, with a linear, impressed midline (a continuation of that of the collum) not reaching the posterior margin, surrounded by a narrow longitudinal, caudally widening  $\perp$ -shaped impression; sublateral parts with shallow Y-shaped impressions (indicated largely by a specific reflection) interrupting the posterior margin (the latter trisinate); the inner arm of each Y terminating in a conspicuous **pronotal pit**. Lateral sides of the midlobe notum turning gradually ventrad (no dorsolateral margin defined), forming vertical upper half of the lateral wall of the prothorax, and joining proepisterna and proepimera. **Hindlobe, dorsum.** Short, lateral margins rounded, posterolateral angles not defined, posterior margin straight. Lateral walls of hindlobe notum turning gradually ventrad (no dorso-lateral margin defined), joining posterior and dorsal margins (posterior half of the latter) of posterior prosupracoxale (proepimeron not developed at this site), and extending posterad and ventrad but not mesad to this supracoxale. (The architecture clearly visible in posterodiagonal view only.) The hindlobe notum forms here a short hanging wall, usually incorrectly called “proepimeral lobe”; posterior margin sharp and moderately convex in lateral view. **Propleuron and prosupracoxal lobes.** Notopleural sulcus absent; episternum and epimeron strip-shaped, distinguished by sculpture, pilosity and concave surface from more dorsal notum and more ventral supracoxal lobes, both being situated within a deep depression above the dorsal margin of anterior prosupracoxale and anterior half of dorsal margin of posterior supracoxale. Episternum delimited from epimeron by a conspicuous **propleural pit**, almost as high as the propleuron itself and

not contiguous with the supracoxal cleft; an internal pleural apophysis arising from the pit. Both anterior and posterior supracoxalia large and high, meeting ventrally in an obtuse angle, the long supracoxal cleft being in line with pleural and notal pits.

**Prosternum** formed by three parts corresponding to collum, eusternum (both strongly sclerotized) and poststernum (semimembraneous), respectively. The collar part continuous with laterodorsal parts of collum, densely pilose, separated from the eusternum by a deep impression. The anterior part of eusternum densely pilose and continuous with equally pilose anteroventral surfaces of anterior supracoxalia, the sharp, perpendicular ventral margins of the latter penetrating onto eusternum whose more posterior part is bare. The most posterior part of eusternum extending laterad along the proacetabula up to the most ventral and most posterior point of posterior prosupracoxale; the posterior margin of eusternum broadly truncate, interrupted sublaterally (at the point closest to proacetabulum) by a pair of unusually wide and deep **prosternal pits**. Poststernum similar to a semisclerotized intersegmental membrane; a pair of stick-like mesal pair of fibulae converging posterad (possibly marking the outline of a desclerotized proxyphus); poststernum bare except for a pair of minute, central, appressed, anteriorly directed setae.

**Pterothorax.** Posterior part of pronotum covering the anterodorsal part of mesothorax while the anteroventral area of mesothorax covering the posteroventral part of prothorax.

**Mesonotum and forewing rudiments.** Mesoprescutum short, mostly covered by pronotum, posterior margin indistinct, arcuate. Mesoscutum large, subtrapezoidal, narrowing posterad, its lateral and posterior margins moderately concave; anterolateral parts extending laterad in front of wing rudiments, and contacting dorsal part of **mesopreepisterna**; lateral margins lath-like (?doubled parapsidal sulci). Posterior part of mesonotum formed by an extensive mesoscutellum composed of three parts: (a) a high, transverse, strongly convex, bulging, slightly transverse central part, its sides rounded, the anterior one emarginate, ante-

rior half with a slightly impressed median, (b) flat, narrow lateral fringes, emitting a pair of anterolateral processes contacting the mesal margins of forewing rudiments, and (c) deeply concave, trough-shaped posterior part, medially fused with metanotum, laterally delimited from the latter by diagonal straight sulci situated within the trough. The strongly convex mesopleuron clearly visible on sides of the mesonotum (in dorsal view), the most posterolateral parts of mesepimeral regions turned onto the dorsum, forming thus its posterolateral sectors (**dorsal mesepisterna**) overlapped by apices of forewing vestiges, and contacting the latter and the lateral extensions of mesopostnotum and anteriormost part of metanotum. (The parts embracing metanotum irregularly delimited from dorsal metepisterna and forming minute C-shaped sclerites.) A pair of deep **mesonotal pits** situated at the site where the dorsal mesepisternum, mesoscutellum and metanotum meet. The longitudinally ellipsoid **forewing rudiments** forming lateral parts of mesonotum; their broad bases (not distinguishable from lateral parts of mesoscutum) associated with mesopreepisterna, mesal margins terminating close to lateral extensions of mesoscutellum; the surface subdivided in an anterior posteromesal moderately convex part, and a posterolateral, black, apically rounded projection produced beyond the mesoscutellar extension over the dorsal mesepisternum.

**Mesopleuron** in anterior 3/4 sharply demarcated dorsally by ventral margin of wing vestige forming here a dorsolateral body margin. A smooth and shiny mesopreepisternum is partly covered by prothorax, contiguous dorsally with the basis of forewing rudiment, and fused ventrally with mesopreesternite; it is clearly delimited from the rugulose major part of pleuron (formed by a fusion of a long mesopostepisternum with precoxale, eusternum, mesepimeron, and with not clearly marked off postcoxale). The postcoxale forms the most posterior part of posterior supracoxale, and does not reach eusternum. Supracoxalia large, their ventral excision acutangular; no pleural sulcus or any other structure developed dorsad to supracoxal cleft. Mesopleuron delimited from metapleuron by a deep groove containing long, crevice-shaped **metathoracic spir-**



**acle.** The posterodorsal part of mesopleuron (of mesepimeral origin) turned onto the dorsum (see under Mesonotum).

#### **Metanotum and hindwing rudiments.**

Metanotum medially fused with mesonotum and delimited from the latter by a smooth deep, concave, steep impression, the intersegmental sulcus developed laterally only. Mesoscutum and mesoscutellum fused, the former recognizable by a bare, polished surface (against sculptured and somewhat pilose surface of mesoscutellum), medial part moderately concave, lateral parts moderately convex, delimited from mesal hindwing margins in posterior 2/3 by **circular muscle scars** and, more posteriorly, by hindwing convexity. Lateral parts of metanotum formed by well-defined **hindwing rudiments**; their lateral margins straight, rounded off, forming lateral sides of the notal areas, slightly extending laterad over the thoracic outline; their rounded, subacute apices produced caudad over the spinously produced posterolateral angles of metanotum; surface irregularly rugulose, mesal margins (excl. protruding distal sector) not delimited by sulci, recognizable by topography, coloration and sculpture only. Anteromesal areas of hindwing vestiges not distinguishable from metascutum & metascutellum except by position of the muscle scar. **Metapostnotum** forming a posterior metanotal strip falling in anterior part steeply posteroventrad, with posterior part flat, extending and turning laterad (behind the spinous subalar projection of mesonotum) and ventrad, coalescing with the metepimeron. The scutopostnotal sulcus obliterate medially, the posterior margin of metapostnotum straight, separated from abdominal tergum 1 by a junctional membrane. Dorsolateral part of metapostnotum with an incomplete, convex, ridge-like apodeme, coinciding for the most part with metanotal-metapostnotal sulcus, and delimiting anteriorly the lateral half of a paired, arcuate, metapostnotal sclerite.

**Metapleuron.** Lateral wall of metathorax formed by (a) ventral part of hindwing vestige, (b) lateral part of metapostnotum, (c) an inversely U-shaped area (including precoxale, dorsal parts of uncertain homology, epimeron and postcoxale) embracing (d)

a strongly inflated metepisternum and anterior supracoxale; (c) and (d) being separated by a deep, inversely U-shaped impression. (a) **Ventral part of hindwing vestige** recognizable as a laterally prominent, rounded off structure, freely projecting caudad, and not delimited by any sulcus. (b) The lateral, ventrally turned part of **metapostnotum** forming a triangular, posterodorsal part of lateral metathoracic wall, fused with its metepimeral part but delimited by a ridge marking an oblique dorsal margin of metepimeron. (c) The **inversely U-shaped part**. The anterior, narrow and deeply sunken postspiracular sector (metaprecoxale and a part of metepisternum?) hardly visible externally, coalescing with metasternum. The dorsal, horizontal, arch-shaped impressed part associated partly with the above hindwing vestiges, partly situated within the inversely U-shaped impression delimiting dorsally the bulging (d)-part, and coalescing caudally with a broad, freely exposed metepimeron markedly widening ventrad. The latter continuing ventrad (approximately up to dorsal 1/3 of anterior metasupracoxale), its ventral margin rounded, forming a minute posterior metasupracoxale, meeting the anterior metasupracoxale under a right angle, the meeting point being marked by a **metapleural pit** situated exactly at the most posteroventral point of the inversely U-shaped impression. No distinct metapostcoxale visible externally. (d) **Metepisternum** extensive and strongly inflated, delimited by the inversely U-shaped impression, its ventral side produced in a large, broad and high anterior metasupracoxale (recognizable by convexity of its surface and sculpture) with broadly rounded ventral and posterior margins, and with posteroventral part turning mesad.

**Pterosterna. Mesosternum** formed by a presternite and eusternum. The presternite (continuous with mesopreepisternum) collar-like, similar to ventral part of prothoracic collum, covering the posterior part of prosternum, delimited from eusternum by a shallow transverse impression. The eusternum (a part of pleuro-eusternal complex) moderately convex (much less than usual in enicocephalids), in posterior part with a broadly and bluntly keeled median, narrowing posterad and continuing onto metastern-



num as a sublinear median ridge. Mesosternum and metasternum completely fused, without any trace of an intersegmental sulcus ventrad to metathoracic spiracle. Mesacetabulum thus fully enclosed by a compact sclerotized area formed by fusion of mesosternum & metasternum & metaprecoxale. Rather inconspicuous mesosternal pits situated just posterior to ventral termination of posterior mesosupracoxale (externally covered by midcoxae).

**Metasternum** formed by two sclerites.

(a) The anterior large **eusternum** posteriorly broadly rounded, situated mesad of metacetabula (i.e. mesad of anterior part of ventral margin of anterior metasupracoxale). Its medial part with a broad elevation turning into a median, rather sharp keel reaching  $3/4$  length of the sclerite, more distal part of the keel diffuse; lateral margins of the elevation and the keel form seemingly a continuation of a curvature of the posterolateral margins of mesosternum (i.e. mesal margins of mesacetabula); posterolateral area of eusternum with a pair of long, strong bristles. The keel internally associated with a broad apodeme emitting long, acute furcal apophysis into each metacetabulum (b) The posterior margin of eusternum internally thickened, emitting postcoxally a rod-like **posterior metacetabular frame** associated internally with an apophysis of metapleural pit, which forms the only metacoxal articulation.

**Abdomen** with a sharp lateral edge (separating dorsal and ventral laterotergites) on segments 2-8 (probably rounded in inflated condition). Ventral and dorsal laterotergites 1 continuous, not mutually delimited.

**Dorsum of abdomen.** All nine terga semimembranous, well delimited, intersegmental sulci straight, only 1-2 and 8-9 arcuate, tergum 1 laterally pointed and 9 anteriorly concave; no longitudinal sulci between mediotergal (MTG) and dorsolaterotergal (DLTG) areas, the latter defined by presence of serial sclerites and/or muscle scars on segments 1-8, DLTG absent on 9; opening of dorsal gland at the anterior margin of MTG 4. MTG 1 turned ventrad (in dry specimens), nearly perpendicular to metapostnotum and MTG 2; MTG 1 with a pair of very large and strongly convex sclerites

(with a delimited posterior lustrous part each), LTG 1 with an indistinct sclerite. Terga 2-8 with series of three pairs of sclerites in the same topographical arrangement (only 2 somewhat different), as follows: (a) large **DLTG sclerite** (2 not well delimited, 3 to 8 gradually increasing in size, length and width), (b) **sublateral muscle scar** in DLTG area (subcircular, discal, mesal to DLTG sclerite on 2; longitudinally arcuate, situated at anterior segment margin on 3-8, distant from DLTG sclerite on 3-5, engulfed on 6-8), (c) **submedial muscle scar** (at anterior margins of MTG 2-8; 2 thickly linear, strikingly long and strongly sclerotized, 3-8 thinner, simply subarcuate, 8 partly contacting LTG sclerite). Tergum 9 small, transverse, uniformly sclerotized, marginal areas slightly thickened, posterolateral angles rounded, posterior margin convex.

**Venter of abdomen.** Ventrites (V) 1-8 well developed, with a system of small sclerites in ventral laterotergal areas (VLTG), tending to increase in size and coalesce in a large VLTG sclerite from V1 to V7. VLTG differentiated from sterna by different sclerite systems and gaps in pilosity, delimitation of VLTG by sulcus obtaining on segments 3, 4 and 8 only. S1 broadly membranous, attached to metasternum and posterior metacetabular frame. Architecture of S2 complex (not well understood); a broadly U-shaped apodeme contacting intersegmental sulcus 2-3, and broadly separate openings of scent glands seem to be present just laterad to this contact. S2-7 with a series of sublateral anterior and posterior sclerites (corresponding in position to those on mediotergites), posterior sclerites of an anterior segment usually coalescing with anterior sclerites of the posterior segment. S6 and S7 each with a large, subtrapezoidal, unpaired medial sclerite as long as the segment. VLTG 8 fully sclerotized. Medial part of V8 formed by a huge, trapezoidal **subgenital plate** widening caudad (sic!), with posterolateral angles separated, and with a minute, simple, pore-like **genital opening** situated within the basal fifth. Segment 9 strikingly transverse, with a ventral, subapical circular opening including a subsphaerical, free **proctiger segments** 10 and 11. **Spiracles** minute, isomorphic, situated ventrally and submarginally on VLTG 2-8.

**Legs.** Forelegs stout, midlegs thin, hindlegs with incrassate femora, longest. Legs relatively long in comparison to narrow body. Trochantines absent in all the acetabula.

**Forelegs** (Figs 5-15). Coxae with bare, matt and finely structured mesal surfaces, suggestive of an adhesive function. Anterodorsal surface with many setigerous tubercles, apical rim around the coxo-trochanteral articulation with many miniature lens-like projections. Trochanter short, without particulars except for three flat areas (dorsal, anterior and ventral); dorsal face with setigerous tubercles. Femur moderately incrassate, smooth. Tibia in dorsal view simply cylindrical, in lateral view compressed and strikingly widening distad, its basiventral face excavate, apic tibial process short; both anterior and posterior faces with many small setigerous tubercles. Ratio length of foretibia to its maximum width 3.05. A bristle comb of 38-40 setae, the two longest ones situated in front of the curved anterodorsal spiniform seta.

**Apic tibial armature** (Fig. 6) consisting of seven slender spiniform setae (two ventral, three subventral, two dorsal), the anterodorsal one strongly curved, directed ventrad and reaching amongst the straight ones. Tarsus cylindrical, all over with setigerous tubercles. **Tarsal armature** (Fig. 6) of 1+1 proximal curved spiniform setae and 1+1 distal semicircular platelets. Claws (Figs 7-8) strong, moderately and gently curved, the posterior one thinner, 3/5 as long as the anterior one, adpressed to the latter. The right larger claw aberrant, with a sinuous extension on its ventral side.

**Foreleg sensilla on coxa, trochanter and femur.** Anteromesally, basal rim of fore-coxa with a **coxal rim organ** (first record in Enicocephalomorpha) consisting of a cluster of two small and four longer, differently directed, straight setae (Figs 14-15). Condylar trochanteral organ of five short setae (Fig. 10). Anterior trochanteral organ (Figs 9, 11) of 5+1 campaniform sensilla (a straight row and an isolated one); posterior trochanteral organ (Figs 12-13) of 4+1 similarly arranged sensilla. Anterior femoral organ (Fig. 9) of four scattered subbasal campaniform sensilla and one widely distant

subdorsal sensillum; posterior femoral organ absent.

**Midlegs.** Coxa, trochanter and femur without particulars, dorsal surface of trochanter long, femur thin, slightly compressed, its anterodorsal face with a series of transverse wrinkles resembling a diluted stridulitrum. Apex of tibia with one short anterior comb and one short posterior comb, each comb starting and terminating with one spiniform seta. Tarsus two-segmented, basal segment very short. Claws isomorphic, with obtusangular basal extension.

**Hindlegs.** Coxa, trochanter, femur and tibia without particulars, generally similar to those of midlegs, only the femur incrassate and distinctly compressed, both anterior and posterior faces nearly flat. Distal armature of tibia with long anterior and long posterior combs nearly surrounding the apex, their marginal setae shorter than on the midtibia. Tarsus and claws as in midtibia.

**Fluctuating asymmetry.** The holotype as well as the female excluded from the type series exhibit a considerable left/right asymmetry concerning the size and shape of forewing and hindwing rudiments, larger foreclaw, and supracoxalia (especially posterior prosupracoxale).

## Discussion

### (1) Relationship of *Heissaptera* and the occurrence of apterous taxa in the Enicocephalidae

The characteristic impressions on the midlobe of pronotum (an  $\perp$ -shaped medial and paired Y-shaped sublateral, the latter two interrupting the posterior margin) are autapomorphic for a clade (*Oncyclocotis*-group) including the W Hemisphere genera *Hoplitocoris* JEANNEL 1942 (subgenera *Hoplitocoris*, *Iphlotocoris* ŠTYS 1981, *Pseudenicocephalus* USINGER 1945), *Oncyclocotis* STÅL 1856 (subgenera *Oncyclocotis*, *Lococytonis* VILLIERS 1969, *Vinsonicoris* VILLIERS 1969), *Embolorrhinus* JEANNEL 1942 (subgenera *Embolorrhinus*, *Ceratotrachelus* USINGER 1945) and *Vuorilinna* ŠTYS 1986; also the W Hemisphere genera *Enicocephalus* WESTWOOD 1837 and *Neoncylocotis* WYGODZINSKY &

SCHMIDT 1991, with the pattern of pronotal impressions more or less reduced (impressions completely lost in *Enicocephalus taeuberi* JEANNEL 1944), belong here. The above classification, particularly the allocation and validity of subgenera, was discussed by ŠTYS (2002b). *Heissaptera* nov.gen. undoubtedly belongs to this complex, although no other apterous species or phenon is known in this clade.

This brings us to the distribution of aptery within the Enicocephalidae (WYGODZINSKY & SCHMIDT 1991; ŠTYS 2002a, 2002b). All obligatorily apterous and extremely micropterous genera belong to Phthiroleptidae (incl. Monteithostolini), while in the Alienatidae only the females are apterous. Of the Enicocephalinae, only *Heissaptera* nov.gen. and the American *Hymenocoris* spp. share the presence of macropterous males and apterous females. However, ŠTYS (1990, 2002a, 2002b) pointed out that two Oriental clades of the Enicocephalomorpha (i.e. Aenictopecheidae: Murphyanellinae and Enicocephalidae: Phallopiratinae, including newly available material of new taxa) are known in the male sex only and that the same applies also for many genera of the Enicocephalinae. This is particularly striking in a geographically coherent group of recently established genera from Middle East and Arabian Peninsula, viz. *Alkowiella* ŠTYS 2002a, *Kulichoderes* ŠTYS 2002a, *Ugloderes* ŠTYS 2002a, *Utukhengal* ŠTYS 2002a, and *Vuorilimna* ŠTYS 1986. Also in a new genus and species from Seychelles, only the males are available. Numerous light-trapped males of *Kulichoderes* spp. (Iran) and *Alkowiella* spp. (Yemen) are available, but not a single female has been found. Consequently, ŠTYS (2002a) hypothesized that females of this group of genera are living in soil and litter, and are flightless, and possibly apterous. Discovery of apterous females in *Heissaptera* nov.gen. supports this assumption.

## (2) Prothorax: notum, pleuron and sternum

Neotenus nature of the thorax of *Heissaptera* nov.gen. allows for some generalizations concerning homology of various components of the thorax. Only the prothorax is scrutinized here. Serially homologous topog-

raphy of different regions of the prothoracic collum suggests, that this continuous ring-shaped, double-layered epidermal (cuticular) evagination with no internal cavity is formed jointly by pronotum (dorsal and dorsolateral parts), proepisternum (lateral tubercles) and prosternum (ventral part). Presence of precollum (cf. ŠTYS & BAŇAŘ 2006), an anterior subdivision or extension of the collum, is probably a universal, overlooked enicocephalid feature.

Dorsal and posterior parts of the lateral body wall of the prothorax are notal in origin, being formed by a simple lateral reflection of the notum (no cryptopleury involved). A large propleural pit is situated just above the supracoxal cleft, and delimits mesally an extremely low proepimeron from an equally low episternum. The pit is homologous to the strongly abbreviated propleural sulcus as also suggested by its internal connection with a pleural apodeme.

Existence of “coxal lobes”, the anteroventral and posteroventral pleural plates covering externally the proximal region of the coxa, and usually meeting each other in a suture called “coxal cleft”, is in the Heteroptera a matter of common knowledge. However, the adjective “coxal” is inappropriate, and the common identification of these structures with episternum, epimeron and pleural sulcus, respectively, is inaccurate. The anterior and posterior supracoxal lobes (= supracoxalia; singular: supracoxale, viz. pro-, meso and metasupracoxale, respectively) are again double-walled epidermal evaginations of episternum and epimeron, respectively. They are usually conspicuous (only the posterior metasupracoxale is often minute, internalized to absent), and meet in a suture called supracoxal cleft. If episternum and epimeron are present as distinct, externally recognizable entities (not fused mutually together or jointly with the notum), they meet in a pleural sulcus. The latter may be very short and take a form (as in *Heissaptera* nov.gen.) of a pleural pit.

Terminologically and factually, the supracoxalia must not be mistaken for precoxale (= precoxal bridge) and postcoxale (= postcoxal bridge), ventral precoxal and postcoxal extensions of proepisternum and

proepimeron, respectively. These regions, particularly the precoxale, do often fuse, without any external landmark, with sternum. (Such a situation does not occur in the prothorax of *Heissaptera* nov.gen.)

The so called “proepimeral lobes” originate from notum, and have nothing in common with pleural epimera. Generality of this statement has to be tested prior to replacement of the misleading term by a new one.

The hindlobe of the pronotum is a double-layered epidermal expansion of the midlobe (a “true” prothoracic notum containing the prothoracic body cavity), and the “proepimeral lobes” are only lateroventral evaginations of the hindlobe, often externally fusing with proepimera and/or posterior prosupracoxalia. In contrast to the collum, no pleural and sternal elements are involved. In the majority of enicocephalomorphans, the left and right “epimeral lobes” are posteroventrally widely separate, leaving the proacetabula “open”. However, for example, in macropterous species of *Henschelia* HORVÁTH (e.g. VILLIERS 1969: fig. 265) the left and right ventral apices of “proepimeral lobes” meet behind the fore coxae, and the proacetabula are thus “closed”. An extreme and bizarre sexually dimorphic condition obtains in *Hymenocoris formicinus* UHLER (cf. WYGODZINSKY & SCHMIDT 1991: ♂♂ – figs 102C, 110B; ♀♀ – figs 102F, 112A) – in macropterous males, the “proepimeral lobes” are slightly enlarged, distant from each other, and the proacetabula are “open”, while in apterous females, the left and right “proepimeral lobes” not only meet each other posterad to the proacetabula but actually fuse together. The proacetabula in females of this species are thus “closed” by a narrow ventral bridge of notal (tergal) origin. At the moment we cannot decide whether also the postcoxale takes place in formation of this postacetabular bridge. Surprisingly, this is a first morphological interpretation of this situation, which is possibly unique in the insects.

### (3) Fusion of pterothoracic segments

The mesonotum and metanotum of *Heissaptera* nov.gen. are medially fused although the lateral sectors of the meso-

metanotal intersegmental sulcus is retained. On the other hand, the mesothoracic and metathoracic eusterna are fused all along their line of contact, and no trace of an intersegmental sulcus is retained. The question of intersegmental fusions in flightless enicocephalomorphans has never been raised and needs a special investigation. A perfunctory look at the literature and specimens suggests that no fusions obtain in Phthirocorinae and Alienatinae, but similar fusions exist probably in females of *Hymenocoris* spp. (Enicocephalinae).

### (4) Developmental and evolutionary nature of wing rudiments; ocelli

Forewing pads of male larvae (fifth instar) of *Heissaptera* nov.gen. do not differ from those of other macropterous Enicocephalidae: the pads are long (completely covering the hindwing pads), mesally contiguous and anapterous (cf. ŠTYS & ŠOBOTNÍK 1999), i.e. the wing rudiments are delimited from the mesoscutal and mesoscutellar cuticle by sulci. Moreover the male larvae are provided with irregularly developed ocellar pigment spots. It can be safely assumed that the males of *Heissaptera* nov.gen. are macropterous and ocellate.

The minute, non-overlapping, widely separate, non-anapterous forewing and hindwing pads of female larva (fifth instar) of *Heissaptera* nov.gen. correspond to the situation normally found in second or third instar enicocephalid larvae. The corresponding adult structures are strongly sclerotized (unlike in larvae), projecting, but only slightly longer (less than would correspond to an expectable difference between adjacent instars), and like in larvae non-articulated and basally confluent with scuto-scutellar cuticle. Female larvae are provided with ocellar spots (like the male larvae), but spots or ocelli are missing in adult females.

How to interpret the above described situations in *Heissaptera* nov.gen., and in the Enicocephalidae generally? The anapterous development of macropterous forewings is undoubtedly peramorphic (accelerated in comparison with ancestral ontogeny) in effect; at present we are unable to say whether a predisplacement or a true acceleration of forewing development is involved (termi-



nology according to ALBERCH et al. 1979). Such a development undoubtedly takes place also in the wings of males of *Heissaptera* nov.gen., still unknown in the adult stage.

A more complex situation exists in *Heissaptera* nov.gen. females. The developmental and metamorphic changes (*sensu* SEHNAL et al. 1996) of the individual body parts are apparently decoupled. The legs and head develop probably at a modal rate, the development of compound eyes is slowed down, and that of ocelli stops at the larval/adult moult. The wing processes in adult females are undoubtedly primary homologues of the larval wing pads as suggested by their positional and relational topography. The adult structures are developmental paedomorphic rudiments (being taken over from the larva, and hence retarded) but at the same time extreme vestiges of wings in structural and anagenetic sense (representing the reductional extreme of pterygopolymorphic morphospace). Without a deeper knowledge of the larval development, it is impossible to assess whether a neoteny or postdisplacement (ALBERCH et al. 1979) is the developmental mechanism concerned. For the time being, a general term **neotenuous aptery** (coined by ŠTYS (1964), meaning retention of larval wing pads or their non-articulating homologues in adults) may cover this and similar situations.

#### (5) Distribution of neotenuous aptery among Heteroptera

Neotenuous aptery in the Enicocephalomorpha is known only in New Caledonian Phthirocorinae: Monteithostolini (ŠTYS 1981, 1982), but monteithostoline wing vestiges in larvae and adults are inconspicuous, loaf-shaped, less wing-like than in *Heissaptera* nov.gen.. The phenomenon is not infrequent in the Gerromorpha (particularly the Gerridae) and apterous Aradidae (no reviews available), and it is an exclusive and inclusive character of all the Polytectidae (Cimicomorpha). In trichophorous pentatomomorphans, the neotenuous aptery occurs in most males and all the females of the Australian Coreidae: Agriopocorinae (ŠTYS 1964; forewing remnants large, of a similar size as in the fourth or fifth instar larvae), and in *Howdenoblissus slateri* ŠTYS from

Colombia (ŠTYS 1991) with forewing and hindwing regions barely recognizable. Undoubtedly, the re-examination of other “apterous” taxa will reveal many such situations.

#### (6) Basiabdominal vibrational organ

The conspicuous modifications of the metapostnotum and abdominal tergum 1 in *Heissaptera* nov.gen. suggest an occurrence of a uniquely modified basiabdominal vibrational organ. Its presence in the Cimicomorpha and Pentatomomorpha has been recently reviewed by GOGALA (2005). Its existence in the other clades of the Neoheteroptera is suggested morphologically (Štys unpubl.) and by records of the corresponding low-frequency vibrations (see ČOKL et al. 2005). An occurrence of this apparatus in basal clades of Heteroptera is being studied by Štys (unpubl.), and the fusional apodemal system between mediotergites 1 and 2 has always been found as its dorsal external component. Incorporation of metapostnotum, as is the case of *Heissaptera* nov.gen., may possibly be apomorphic for some apterous taxa and/or phena. In any case, the mere presence of basiabdominal vibrational system in the enicocephalomorphans suggests its synapomorphic nature in terms of all heteropteran clades. We cannot say whether it is apomorphic for Heteropteroidea (i.e. Coleorrhyncha and Heteroptera), since we have not yet seen the details of its study in the Peloriidae (HOCH et al. 2006).

#### (7) Position of openings of adult scent glands

If the tentative observation on presence of widely separate paired opening of “metathoracic” scent glands in the posterior part of abdominal ventrite 2 is correct, and if the basiabdominal enicocephalid and stemmocryptid (ŠTYS 1983) glands are homologous to metathoracic glands of other Heteroptera, then the position discovered in *Heissaptera* nov.gen. would be possibly most plesiomorphic among Heteroptera. This issue will be considered elsewhere (Štys & Cassis in prep.). We have to point out that while the enicocephalid orifices are junctional or abdominal, those of the Stemmocryptidae are metasternal.

The points (6) and (7) are possibly functionally associated: apterous litter inhabiting females need an efficient acoustic and chemical signaling to flying males, and shift of gland openings from abdominal sternum 1 (usual position in Enicocephalinae) could stop any possible interference with vibrational mechanism.

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## Zusammenfassung

Eine neue, monotypische Gattung der Enicocephalomorpha (Enicocephalidae, Enicocephalinae), *Heissaptera janaki* nov.gen. et nov.sp., wird aus Mauritius auf Grundlage neotäner apterer Weibchen beschrieben, die in der Streuaufgabe eines Gebirgswaldes gesammelt wurden. Die neue Gattung gehört zu einer Gruppe von Gattungen mit lateralen Y-förmigen und medialen L-förmigen Eindrücken (oder deren Rudimenten) am mittleren Lobus des Pronotum. Die Anatomie des Exoskeletts des Thorax wird detailliert beschrieben. Die pterothorakalen Segmente sind an den notalen und sternalen Regionen verschmolzen. Rudimente der larvalen Vorder- und Hinterflügelanlagen bleiben als kleine, nicht gelenkig verbundene Loben erhalten. Die Beziehungen der neuen Gattung, Auftreten von Apterie bei Enicocephalidae und neotäne Apterie bei Heteroptera werden zusammengefasst und die Morphologie des Prothorax diskutiert. Die "Proepimeralen Loben" werden als Regionen notalen, nicht

pleuralen, Ursprungs identifiziert. Das Metapostnotum und das erste abdominale Mediotergit sind modifiziert als Teile eines einzigartigen, basiabdominalen Vibrationsorgans; das Auftreten eines Vibrationssystems an der Basis des Abdomens ist eine Synapomorphie der Heteroptera.

## References

- ALBERCH P., GOULD S.J., OSTER G.F. & D.B. WAKE (1979): Size and shape in ontogeny and phylogeny. — *Paleobiology* **5**: 296-317.
- ČOKL A., VIRANT-DOBERLET M. & M. ZOROVIC (2005): Sense organs involved in the vibratory communication of bugs. — In: DROSOPoulos S. & M.F. CLARIDGE (Eds), *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution*. Taylor & Francis, Boca Raton: 71-80.
- GOGALA M. (2005): Vibratory signals produced by Heteroptera – Pentatomorpha and Cimicomorpha. — In: DROSOPoulos S. & M.F. CLARIDGE (Eds), *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution*. Taylor & Francis, Boca Raton: 275-296.
- HOCH H., DECKERT J. & A. WESSEL (2006): Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). — *Biology Letters*, Paper 1744-957X (Online Abstract).
- SEHNAL F., ŠVÁCHA P. & J. ZRZAVÝ (1996): Evolution of insect metamorphosis. — In: GILBERT L.I., TATA J.R. & B.G. ATKINSON (Eds), *Metamorphosis. Postembryonic Reprogramming of Gene Expression in amphibian and insect cells*. Academic Press, New York (N.Y.): 3-58.
- ŠTYS P. (1964): On the morphology and taxonomy of Agriopocorinae (Heteroptera: Coreidae). — *Acta Soc. Entomol. Českoslov.* **61**: 25-38.
- ŠTYS P. (1981): A new relict subfamily, genus and species of Enicocephalidae from New Caledonia (Heteroptera). — *Acta Entomol. Bohemoslov.* **78**: 412-429.
- ŠTYS P. (1982): New genus, two new species, females and larvae of Monteithostolinae from New Caledonia (Heteroptera, Enicocephalidae). — *Acta Univ. Carol. – Biol.* **1980**: 491-515.
- ŠTYS P. (1983): A new family of Heteroptera with dipsocoromorphan affinities from New Guinea. — *Acta Entomol. Bohemoslov.* **80**: 256-292.
- ŠTYS P. (1990): Enicocephalomorphan and dipsocoromorphan fauna of W Palaearctic: Composition, distribution, and biology (Heteroptera). — *Scopelia, Suppl.* **1**: 3-15.
- ŠTYS P. (1991): First apterous genus and species of Lygaeidae: Blissinae (Heteroptera). — *Acta Entomol. Bohemoslov.* **88**: 265-271.

- ŠTYS P. (2002a): New enicocephaline genera similar to *Systelloderes* (Heteroptera: Enicocephalidae). — Acta Univ. Carol. – Biol. **45**: 319-338.
- ŠTYS P. (2002b): Key to the genus-group taxa of the extant Enicocephalomorpha of the World, their list, and taxonomic changes (Heteroptera). — Acta Univ. Carol. – Biol. **45**: 339-368.
- ŠTYS P. & P. BAŇAŘ (2006): A new species of *Neoncylocotis* (Heteroptera, Enicocephalidae) from Ecuador. — Polske Pismo Entomol. **75**: 169-183.
- ŠTYS P. & J. ŠOBOTNÍK (1999): Comments on classifications of insect ontogenies, and occurrence of proneometabolous wing development in termite genus *Prorhinotermes* (Hexapoda: Isoptera). — Acta Soc. Zool. Bohem. **63**: 483-492.
- VILLIERS A. (1969): Révision des Hémiptères Henicocephalidae Africains and Malgaches. — An. Mus. Afrique Centr., Ser in 8°, Sci. Zool., Tervuren **176**: 1-232.
- WYGODZINSKY P.W. & K. SCHMIDT (1991): Revision of the New World Enicocephalomorpha (Heteroptera). — Bull. Am. Mus. Nat. Hist. **200**: 1-265.

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